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Size and shape information serve as labels in the alarm calls of Gunnison's prairie dogs *Cynomys gunnisoni*

C. N. SLOBODCHIKOFF[1*], William R. BRIGGS[1], Patricia A DENNIS[1], Anne-Marie C. HODGE [2,3]

[1] Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011, USA

[2] Department of Biological Sciences, Auburn University, Auburn, Alabama 36849, USA

[3] Present Address: Department of Zoology and Physiology, University of Wyoming, Laramie, WY82071, USA

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Abstract Some animals have the capacity to produce different alarm calls for terrestrial and aerial predators. However, it is not clear what cognitive processes are involved in generating these calls. One possibility is the position of the predator: Anything on the ground receives a terrestrial predator call, and anything in the air receives an aerial predator call. Another possibility is that animals are able to recognize the physical features of predators and incorporate those into their calls. As a way of elucidating which of these mechanisms plays a primary role in generating the structure of different calls, we performed two field experiments with Gunnison's prairie dogs. First, we presented the prairie dogs with a circle, a triangle, and a square, each moving across the colony at the same height and speed. Second, we presented the prairie dogs with two squares of differing sizes. DFA statistics showed that 82.6 percent of calls for the circle and 79.2 percent of the calls for the triangle were correctly classified, and 73.3 percent of the calls for the square were classified as either square or circle. Also, 100 percent of the calls for the larger square and 90 percent of the calls for the smaller square were correctly classified. Because both squares and circles are features of terrestrial predators and triangles are features of aerial predators, our results suggest that prairie dogs might have a cognitive mechanism that labels the abstract shape and size of different predators, rather than the position of the predator [*Current Zoology* 58 (5): 741–748, 2012].

Keywords Gunnison's prairie dogs, Prairie dogs, Alarm calls, Referential communication

A number of animal species have been shown to incorporate categorical information into their alarm calls. Some animals have two types of calls, one for a terrestrial category and another for an aerial category of predators. Examples of species with two types of alarm calls are: many ground squirrels (*Spermophilus* spp.) (Owings and Hennessy, 1984); Richardson's ground squirrels *Urocitellus richardsonii* (Davis, 1984; Hare and Atkins, 2001; Swan and Hare, 2008); chickens *Gallus gallus domesticus* (Gyger et al., 1987; Evans et al., 1993; Evans and Evans, 1999); tree squirrels *Tamiasciurus hudsonicus* (Greene and Meagher, 1998); dwarf mongooses *Helogale undulata* (Beynon and Rasa, 1989); and suricates *Suricata suricatta* (Manser, 2001; Manser et al., 2001).

Several species have vocalizations for different species or multiple categories of predators. Such calls have been found in: vervet monkeys *Chlorocebus pygerythrus*, with calls for three different types of predators, snake or python, large cat species or leopard, and eagle (Cheney and Seyfarth, 1990); Diana monkeys *Cercopithecus diana* and Campbell's monkeys *Cercopithecus campbelli*, with calls for leopards *Panthera pardus* and crowned-hawk eagles *Stephanoaetus coronatus* (Zuberbühler, 2000, 2001); and Gunnison's prairie dogs *Cynomys gunnisoni*, with calls for coyotes *Canis latrans*, domestic dogs *Canis familiaris*, humans *Homo sapiens*, and red-tailed hawks *Buteo jamaicensis* (Kiriazis and Slobodchikoff, 2006; Placer and Slobodchikoff, 2000, 2001, 2004; Placer et al., 2006; Slobodchikoff, 2002; Slobodchikoff and Placer, 2006).

One difficulty in understanding the nature of these calls is that it is not clear what information animals are using to structure the alarm calls. Is it size, shape, and color of the predators, is it something to do with the position of the predators, or is it instructions for escape? For example, in terrestrial vs. aerial predator alarm calls, it is possible that the position of a predator might determine the nature of the alarm call. Anything on the ground could elicit a terrestrial predator call, and any-

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* Corresponding author. E-mail: Con.Slobodchikoff@nau.edu

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thing in the air could elicit an aerial predator call. This appears to be the case with chicken alarm calls (Evans et al., 1993). With the three types of alarm calls produced by vervet monkeys, anything low to the ground could produce a snake call, anything on the ground with a somewhat higher profile could produce a leopard call, and anything in the air could produce an eagle call (Cheney and Seyfarth, 1990). This can be refined through stimulus discrimination learning so that eventually the animals are responding with alarm calls only to pythons, leopards, and eagles.

Another difficulty is that some animals respond with graded alarm calls depending on the urgency of the situation, which has been termed response-urgency (Owings and Morton, 1998). For example, yellow-bellied marmots *Marmota flaviventris* do not have different calls for different categories of predators, but instead vary their rate of calling depending on the distance that they are from the predator (Blumstein and Armitage, 1997; Collier et al., 2010). Other animals such as meerkats *Suricata suricatta* and Richardson's ground squirrels have both categorical and response- urgency elements encoded in their alarm calls or can assess the urgency of a situation by the number of callers (Furrer and Manser, 2009; Sloan and Hare, 2008).

A partial answer to this problem lies in elucidating whether alarm calls contain information describing the physical features of predators. Among mammals, Gunnison's and black-tailed prairie dog *Cynomys ludovicianus* alarm calls contain information about size and shape of humans intruding into a prairie dog colony, and contain descriptive labels about the color of clothes that the human intruders were wearing (Slobodchikoff et al., 1991; Frederiksen and Slobodchikoff, 2007; Slobodchikoff et al., 2009a). Richardson's ground squirrels *Urocitellus richardsonii* can communicate the direction of travel of a predator (Thompson and Hare, 2010), and banded mongoose *Mungos mungo* can provide information about the degree of risk (Furrer and Manser, 2009). Among birds, chickens can provide information about the size, speed, and proximity of a predator (Wilson and Evans, 2012), and chickadees (*Poecile atricapillus* and *P. carolinensis*) can provide information about the size of different predators (Templeton et al., 2005; Soard and Ritchison, 2009).

In our present study, we attempted to address this problem by asking whether Gunnison's prairie dogs would respond with different alarm calls to several abstract unfamiliar geometric shapes that were presented to them as two-dimensional models that moved across the colony at a constant speed. We did two experiments. In the first experiment, we used a triangle, a circle, and a square that were presented randomly to the prairie dogs by pulling each shape across the colony from one tower blind to another. In the second experiment, we used a larger square and a smaller square shape that were presented randomly and pulled across the colony in the same way as in the first experiment. In these experiments, our hypothesis was that if the prairie dogs were responding by incorporating different information into their alarm calls for each shape, then we expected to see significant differences among the alarm calls for the different shapes. The null hypothesis was that if the prairie dogs were responding to the position of the shapes, then we expected to see no significant differences among any of the alarm calls for any of the shapes.

If the prairie dogs incorporated acoustic differences into their alarm calls for the different shapes, this could suggest the possibility that the prairie dogs are capable of forming cognitive categories of the different geometric shapes, and can incorporate information about those categories into their alarm calls. On the other hand, if there are no differences in the alarm calls to any of the shapes, then the possibility exists that the alarm calls to the shapes might represent a positional response to something that is unfamiliar, or simple expressions of fear at seeing a novel stimulus. In this latter case, we would not expect to find any significant differences between any of the calls elicited for the different shapes and the different sizes.

1 Materials and Methods

1.1 Study animal

Gunnison's prairie dogs are large, diurnal rodents in the ground-squirrel family Sciuridae, with adults having an average weight of 250–1100 grams. The animals are colonial, living in "towns" that contain extensive burrow systems to which the prairie dogs retreat from predators, and where they spend the night. The colonies are subdivided into territories, with each territory containing one to several adult males and one to several adult females and young of both sexes (Travis and Slobodchikoff, 1993). There are five species of prairie dogs, all found exclusively in North America. Gunnison's prairie dogs are found in Arizona, Colorado, New Mexico, and Utah, inhabiting mountain valleys and plateaus at elevations of 1830–3660 m (Slobodchikoff et al., 2009b).

1.2 Study site and experimental design

We did the experiments in a large colony of Gunni-

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son's prairie dogs, located just outside the city limits of Flagstaff, Arizona, at 35N 11' 41"× 111W 33' 42" at an elevation of 2064 m, from 28 May to 15 July, 2007. The colony was 14.88 hectares in size and contained approximately 300 animals.

We did two experiments. The first experiment exposed the prairie dogs to three different black shapes, all of the same height (0.91 m). The shapes we used were a square, a circle, and a triangle, all constructed of cardboard and painted black. The area of the square was 0.84 m^2, the area of the circle was 0.66 m^2, and the area of the triangle was 0.42 m^2. The second experiment exposed the prairie dogs to the large black square used in the previous experiment and to a smaller black square measuring 0.61 m in height and an area of 0.37 m^2.

We erected two Big Game Vertex Combo platform-stand hunting blinds as observation towers within the colony, and set up a pulley system between them. The blinds were 2.13 meters tall with 1.22 meter square platforms, and were spaced 90 meters apart. An additional blind was located on the ground 30 meters from the center of a rope that stretched between the towers. The pulley apparatus used a rope (0.95 centimeters in diameter) positioned 2.1 meters above the ground. While inside the blinds, the individual shapes were attached to the rope using mini-carabineers and situated with the largest side next to the rope. We used an automatic drill to turn the pulley, in order to keep the shapes moving at a uniform speed of 0.60 meters per second.

The shapes were sent across only from west to east; they were not passed back along the pulley to the original tower. The towers were set up in parallel orientations at each site, to control for effects of shadows as the shapes travelled across the site. We selected focal animals by proximity to the observation stations and the path of the pulley, and recorded the alarm calls elicited by each stimulus. Microphones were positioned an average of approximately 30 meters from the prairie dogs, with small variations of recording distances due to the distribution of burrows and movements of individual animals while foraging.

We conducted experimental trials in each of five different locations within the study site, in order to collect data from individuals inhabiting different territories observed within the colony, to ensure that no one individual prairie dog was recorded more than once. After the towers and pulley were set up in a new location, they were left unvisited for one day to allow the prairie dogs to habituate to their presence. All trials were conducted between 05:30 and 08:00 h (MST) with similar wind, cloud cover and dew point. On sampling days, we set up the equipment before the prairie dogs emerged from their burrows for morning foraging. After the first prairie dog emerged from a burrow, a 45 minute habituation period was allowed to pass before the first stimulus object was introduced. Between each trial (a run of one shape across the site), there was a 45 minute habituation period. The order of shapes presented to the colony was randomized for each trial and each shape was only used once per day.

Recording started when the stimulus first appeared from the first blind, and ended when the shape reached the second blind and was removed from the view of the colony. Each trial was recorded to a separate audio file, and only the alarm call from a single focal animal was analyzed from each trial.

We recorded calls with Marantz PMD-66 digital recorders, using Sennheiser ME 66 microphones with Sennheiser K-6 powering modules. All recordings were made using uncompressed PCM (Pulse Code Modulation). File format was .WAV, and sample frequency was recorded at a rate of 48 kHz (48000 samples per second). The bit rate was constant at 768 kbps. Recordings were made in monaural mode. No filters or limiters were used during the recording process. Alarm calls were recorded onto Lexar CF memory cards.

1.3 Data analysis

We analyzed sound recordings using Adobe Audition 2.0 and Cornell Laboratory of Ornithology's Raven Pro for Windows, Version 1.3, Build 18. Individual calling bouts were isolated into separate files with the Adobe Audition. We analyzed the individual calls with Raven Pro, using a Hanning window, with a spectrum window size of 512 samples with a 3 db filter bandwidth of 124 Hz. The grid spacing was 86 Hz, and the time grid was at 50% with a Hop window of 256 samples.

On individual spectrograms, following the methods of Slobodchikoff et al. (1991), we measured nine call parameters: fundamental frequency (FF), dominant harmonic frequency (DHF), supradominant harmonic frequency (SHF), total time of call (TT), time of first half and second halves of the ascending part of the call (TAS1 and TAS2), slopes of first and second halves of the ascending parts of the call (AS1 and AS2), time of first, second, third, and fourth quarters of descending part of the call (TDS1, TDS2, TDS3, and TDS 4, respectively), and slopes of first, second, third, and fourth quarters of the descending parts of the call (DS1, DS2, DS3, and DS4) (Fig. 1).

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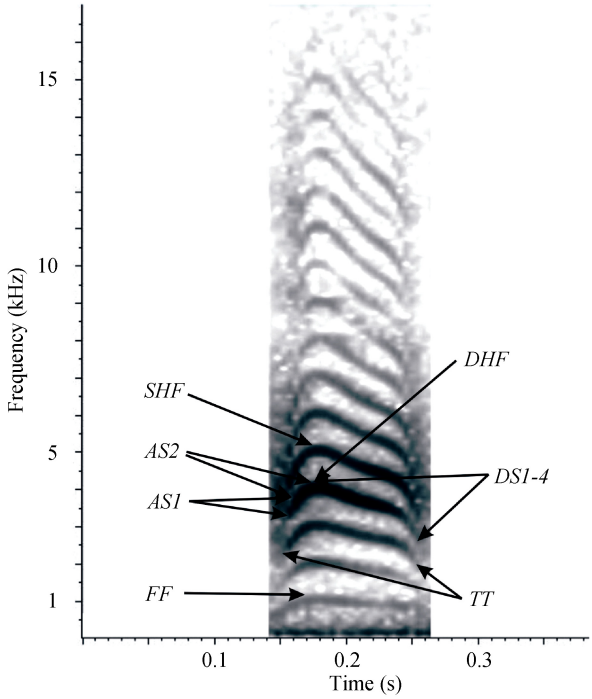

Fig. 1 Diagram of call components used for analysis

FF = Fundamental Frequency, DHF = Dominant Harmonic Frequency, SHF = Supra-Dominant Harmonic Frequency, TT = Total Time of call, TAS1 = Time of first half of ascending call, TAS2 = Time of second half of ascending call, AS1 = Slope of first half of ascending call, AS2 = Slope of second half of ascending call, TDS1 = Time of first quarter of descending call, TDS2 = Time of second quarter of descending call, TDS3 = Time of third quarter of descending call, TDS4 = Time of fourth quarter of descending call, DS1 = Slope of first quarter of descending call, DS2 = Slope of second quarter of descending call, DS3 = Slope of third quarter of descending call, DS4 = Slope of fourth quarter of descending call.

We analyzed the calls with Discriminant Function Analysis (DFA) using SPSS software, version 15.0, with the cross-validation option. To avoid the possibility of pseudoreplication, only a single alarm call from each individual prairie dog was used in the analysis. For the first experiment, we analyzed the calls elicited by the three different shapes, square, circle, and triangle. Sample sizes for these shapes were 15 prairie dog calls for the square, 23 prairie dog calls for the circle, and 24 prairie dog calls for the triangle. For the second experiment, calls elicited by the large and small squares were compared. Sample sizes for these shapes were 16 prairie dog calls for the large square and 9 prairie dog calls for the small square. We analyzed the relationship of the variables to one another for each shape with Principal Components Analysis (PCA) using SPSS version 15.0.

2 Results

2.1 Escape behaviors

All of the prairie dogs in the two experiments exhibited a single escape strategy: run to their burrows. This same escape strategy was observed regardless of the shape or size of the object that was eliciting the alarm calls.

Shapes

The DFA analysis showed that the discrimination for shapes was significant (P<0.000, Wilks' Lambda = 0.462, $F_{10,106}$ = 4.987). The DFA extracted two discriminant functions, with function 1 explaining 88.9% of the variance, and function 2 explaining 11.1% of the variance, for a cumulative total of 100% of the variance explained by the two functions. Spectrograms for the alarm calls to the different shapes are shown in Fig. 2 A–D.

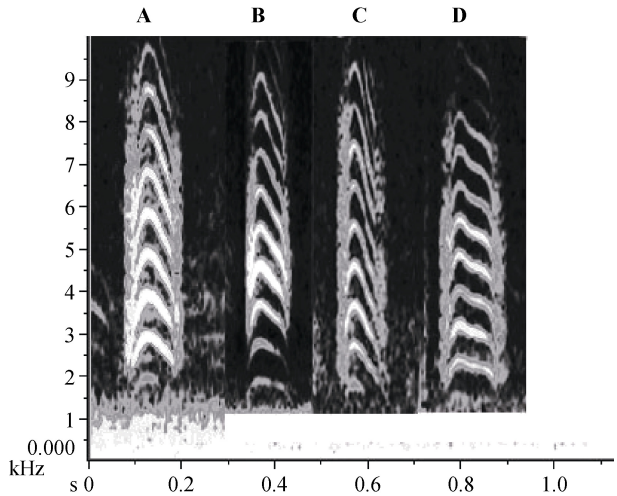

Fig. 2 Gunnison's prairie dog alarm calls for different shapes and sizes

A. Call for circle. **B**. Call for triangle. **C**. Call for large square. **D**. Call for small square.

In the shape experiment, the DFA results suggested that prairie dogs appeared to be able to encode information for the different novel geometric shapes into their alarm calls (Fig. 3). There was an overall classification accuracy of 69.4% (Table 1). Alarm calls for circle were correctly classified for 82.6% of the calls elicited by the circle shape, the calls for triangle were correctly classified for 79.2% of the calls elicited by the triangle shape, and the calls for square were correctly classified for 33.3% of the calls elicited by the square shape. The comparison of the calls for circle vs. triangle was highly significant (P<0.000, $F_{5,\ 53}$ = 9.676,), as was the comparison of calls for triangle vs. square (P=0.004, $F_{5,53}$ =4.031). The comparison for calls for square vs. circle was not significant (P=0.096, $F_{5,53}$=1.984). However, the combined discrimination for circle and square was 73.3 percent of the calls. Cross-validation showed similar results.

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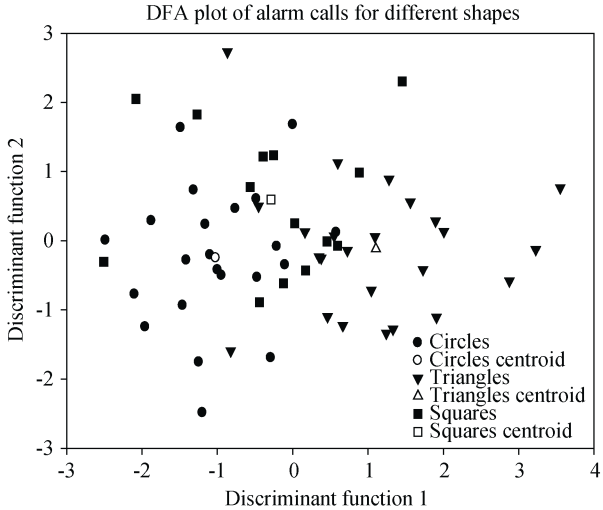

Fig. 3 Discriminant Function plot for the distribution of the alarm call scores for the circle, triangle, and large square shapes

Some of the variables were significant to the analysis in discriminating between shapes, and others were not. Variables that were significant were AS1 (ascending slope 1), and TDS1, TDS2, TDS3, TDS4 (time of descending slopes 1–4). The remaining variables did not have a significant contribution to the discrimination among the different shapes. However, a PCA analysis of the relationship of the variables to one another along three principal component axes showed that the distribution of variables differed for each shape, although an inspection of the distribution of variables for the circle and the square shows that the variables had greater similarity of position along the three principal components axes than the variables for circle and triangle (Figs. 4–6).

Size

The DFA analysis showed that the discrimination for size was significant (P<0.000, Wilks' Lambda = 0.272, $F_{5,20}$=10.55). The DFA extracted one discriminant function, which explained 100% of the variance.

There was an overall classification accuracy of 96.2% (Table 2). Alarm calls for the large square were correctly classified for 100% of the calls elicited by the large square shape, and the calls for the small square were correctly classified for 90% of the calls elicited by the small square shape. Similar classification percentages were obtained for the cross-validation. The comparison of the calls for the large square vs. the small square was highly significant (P<0.000, $F_{5, 20}$=10.55).

Some of the variables were significant to the analysis in discriminating between sizes, and others were not. Variables that were significant were AS2 (ascending slope 2), DS2 (descending slope 2) and TDS1, TDS2, TDS3 (time of descending slopes 1–3). The remaining variables did not have a significant contribution to the discrimination between the two sizes.

Table 1 Classification accuracy for alarm calls elicited by each of three geometric shapes (square, circle, and triangle) measuring 0.91 m tall

		shape	Predicted Group Membership			
			Square	Circle	Triangle	Total
Original	Count	Square	5	6	4	15
		Circle	2	19	2	23
		Triangle	1	4	19	24
	%	Square	33.3	40.0	26.7	100.0
		Circle	8.7	82.6	8.7	100.0
		Triangle	4.2	16.7	79.2	100.0
Cross-validated[a]	Count	Square	2	8	5	15
		Circle	3	17	3	23
		Triangle	2	4	18	24
	%	Square	13.3	53.3	33.3	100.0
		Circle	13.0	73.9	13.0	100.0
		Triangle	8.3	16.7	75.0	100.0

[a] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case. 69.4% of original grouped cases correctly classified. 59.7% of cross-validated grouped cases correctly classified.

3 Discussion

The results suggest that prairie dogs are able to in-

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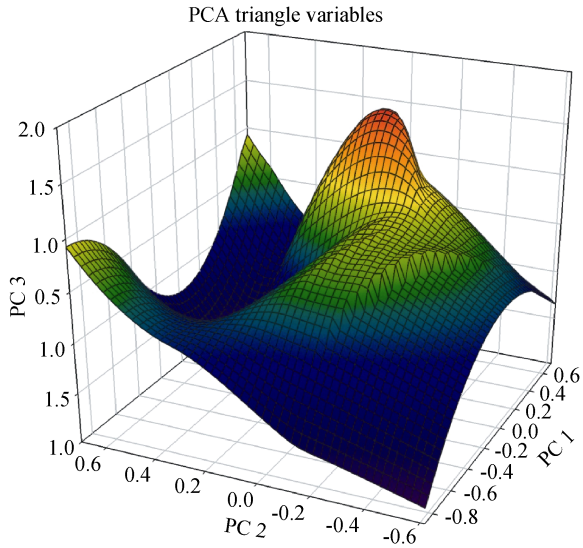

Fig. 4 Principal Components Analysis (PCA) of position of variables in 3-dimensional component space for the alarm calls elicited by the triangle shape

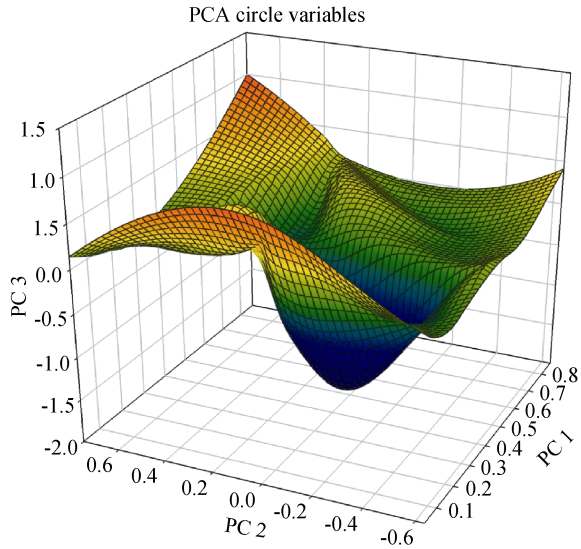

Fig. 5 Principal Components Analysis (PCA) of position of variables in 3-dimensional component space for the alarm calls elicited by the circle shape

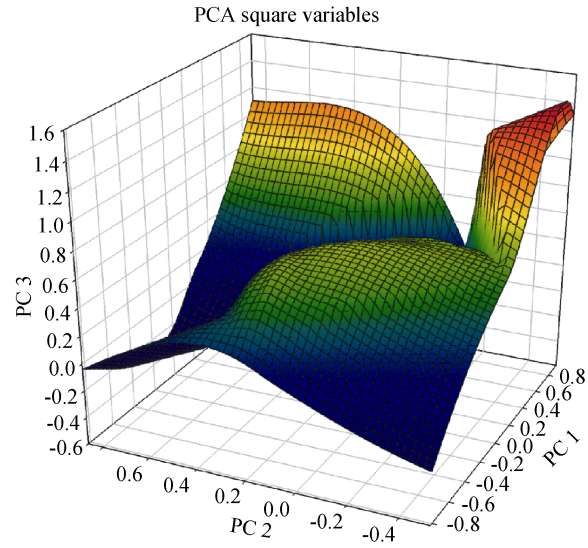

Fig. 6 Principal Components Analysis (PCA) of position of variables in 3-dimensional component space for the alarm calls elicited by the square shape

corporate descriptive information about size and shape into their alarm calls. Previous studies have demonstrated referential specificity in regards to predator category (e.g., humans, coyotes, domestic dogs, red-tailed hawks, Kiriazis and Slobodchikoff, 2006) and physical attributes such as color, size, and shape (Slobodchikoff et al., 1991; Slobodchikoff et al., 2009b), but these studies have used live animals or humans as the eliciting stimuli. Thus, there was always the possibility that the prairie dogs responded to subtle differences in the behavior of different predator species, or different human individuals, as a basis for incorporating acoustic differences into their alarm calls. In the present study, we eliminated all variations in the behavior of the eliciting stimuli by making all of the stimuli travel across the prairie dog colony at the same constant height and the same constant speed.

Table 2 Classification accuracy[a,c] for alarm calls elicited by each of two sizes of square shape

Ref			Predicted Group Membership		Total
			Large	Small	
Original	Count	Large	16	0	16
		Small	1	9	10
	%	Large	100.0	0.0	100.0
		Small	10.0	90.0	100.0
Cross-validated[b]	Count	Large	15	1	16
		Small	1	9	10
	%	Large	93.8	6.3	100.0
		Small	10.0	90.0	100.0

[a] 96.2% of original grouped cases correctly classified.
[b] Cross validation is done only for those cases in the analysis. In cross validation, each case is classified by the functions derived from all cases other than that case.
[c] 92.3% of cross-validated grouped cases correctly classified.

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From this, we can conclude with some confidence that the prairie dogs were responding to differences in the size and the shape of the eliciting stimuli, rather than to differences in the behavior of the stimuli. Three of the time variables (TDS1, TDS2, TDS3) were the same variables for distinguishing between shapes and between sizes, but one ascending slope variable (AS1) and one time variable (TDS4) were significant for shapes, and two different slope variables, ascending slope 2 (AS2) and descending slope 2 (DS2) were significant for sizes. The differences between shapes and between sizes appear to be encoded in these variables. Also, the PCA analysis showed that the relative positions of the variables in three-dimensional principal component space were somewhat more similar for the circle and the square than they were for the circle and the triangle, although all three shapes had clearly different variable-surfaces. If the prairie dogs were simply responding to the differences in the areas of the shapes, rather than to the different shapes themselves, then we would have expected that the variables that were significant in the discrimination between the large square and the small one would also have been the significant ones in discriminating between the square, the circle, and the triangle. Clearly, that was not the case.

A key point is that the shapes we used in our experiments were novel objects that the prairie dogs had not seen previously. The animals' consistent response with acoustic differences in their alarm calls to the different shapes suggests that the prairie dogs might have some form of cognitive mechanism for encoding descriptive information, even if they have not seen a particular object or a particular predator previously. A previous study showed that prairie dogs can incorporate descriptive information about an oval silhouette stimulus (Ackers and Slobodchikoff, 1999). Perhaps the prairie dogs have a cognitive mechanism that can distinguish between circular or rectangular shapes that are more characteristic of ground predators, and triangular shapes that are more characteristic of aerial predators. In this respect, perhaps the relative inability of the prairie dogs to encode descriptive information about the large square shape (when contrasted with circle and triangle) might be due to the lack of square-shaped predators under natural conditions.

One question that arises is, why should size matter? What difference should it make to the prairie dogs whether the predator was a large one or a smaller one? We know from previous studies that prairie dogs can incorporate information into their alarm calls about the size and shape of a predator (Slobodchkoff et al., 1991) and about the predator's color (Slobodchikoff et al., 2009a). One possibility might be that these descriptive labels describe either the individual identity of a predator or some aspect of that individual predator's behavior. Because prairie dogs live in spatially-fixed colonies, the same individual predators come on a daily basis to hunt the prairie dogs (Slobodchikoff et al, 2009b). Some of these predators hunt in different, individually-distinct ways. For example, some coyote individuals hunt by running through a prairie dog colony and charging at any prairie dog that they see. Other individual coyotes hunt by lying down next to a burrow where they saw a number of prairie dogs, and waiting there for up to an hour for an unwary prairie dog to emerge (Leydet, 1977). Perhaps a description of the predator provides the prairie dogs with cues about that predator's hunting style.

The results show that the prairie dogs are responding to the different shapes and sizes with labels, rather than instructions for escape. For all of the shapes and sizes, the responses of the prairie dogs were the same: run to their burrow. This run-to-burrow escape response was different from the different escape responses that prairie dogs have to different species of predators, where a human elicits running to the burrow and diving inside, while a coyote elicits running to the burrow and standing on the lip of the burrow, watching the coyote, and a low-flying hawk elicits a localized running to the burrows from the prairie dogs in the immediate flight path of the hawk (Kiriazis and Slobodchikoff, 2006). For future study, it would be interesting to see if the escape response times differed between the different geometric shapes.

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